Biodivers Conserv (2016) 25:2543–2561
DOI 10.1007/s10531-015-1020-7

ORIGINAL PAPER

Spontaneous steppe restoration on abandoned cropland in Kazakhstan: grazing affects successional pathways

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Received: 20 April 2015 / Revised: 9 September 2015 / Accepted: 23 October 2015 /

Abstract After the collapse of the Soviet Union in 1991, 12 million ha of cropland were abandoned in the steppe zone of Kazakhstan. At the same time livestock numbers crashed, leaving large areas of steppe without any grazing. We aimed to investigate, to which degree spontaneous succession on former cropland leads to the restoration of native steppe vegetation, and how this process is influenced by changing grazing patterns. We recorded biomass and vegetation characteristics as well as local soil and landscape variables in 151 quadrats of 100 m^2, covering 89 plots on former cropland abandoned in the early 1990s and 62 reference plots of near-natural steppe grassland that was never ploughed. About half of the plots of each category were located in a remote region where grazing has been absent for ca. 20 years, whereas the other half was located in a region with moderate livestock grazing. While there were no differences in the diversity, structure and plant life form composition of currently grazed and un-grazed near-natural steppe grasslands, corresponding successional plots on abandoned arable land exhibited significant differences. Grazed plots on former fields showed higher species richness and a higher cover of dwarf shrubs (mostly *Artemisia* spec.), ruderals and perennial herbs. At the same time, immigration of typical steppe species was much more successful. Contrary, in the absence of any grazing we found species-poor swards dominated by *Stipa lessingiana* and *Leymus*

Communicated by Péter Török.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-015-1020-7) contains supplementary material, which is available to authorized users.

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ramosus exhibiting an increasing frequency of wildfires due to litter accumulation. After 15–20 years, secondary steppe grasslands still differed substantially from their near-natural references. Our results suggest that grazing is mandatory to fully restore the original near-natural steppe vegetation and the underlying processes of pyric herbivory.

Keywords Succession · Fire · Pyric herbivory · Dispersal limitation · Novel ecosystems · *Stipa*

Introduction

Globally, temperate grasslands and their specific biodiversity have suffered disproportionally from large-scale conversion into cropland and improved pastures (Hoekstra et al. 2005). This also applies to the western Eurasian steppe belt that stretches from Ukraine with outliers in the Pannonian Basin to the Altai Mountains. While the European part west of the Ural mountains had been almost entirely converted into cropland until the end of the 19th century, in the Asian part in southern Western Siberia and northern Kazakhstan 35 million ha of native steppe grasslands were ploughed for cereal cropping during the 'Virgin Land Campaign' in the Khrushchev era between 1953 and 1961. With the dissolution of the Soviet Union in 1991, institutional change, the transition from a state-controlled to a market economy, and the associated collapse of the former state farm system led to rural depopulation and the abandonment of vast tracts of former cropland (Alcantara et al. 2013; Kamp et al. 2011; Prishchepov et al. 2012).

In Kazakhstan, the area of arable land decreased by 50 % between 1991 and 2000, leaving 12 million ha of former cropland abandoned (De Beurs and Henebry 2004; Kamp et al. 2012). Livestock numbers crashed during the same period, with declines of 80 % in sheep and up to 50 % in cattle and horses (Kamp et al. 2012; Robinson and Milner-Gulland 2003). Since 2000, many steppe areas in northern Kazakhstan were re-cultivated, but governmental statistics suggest that at least 7 million ha of former cropland are still abandoned (Kazakhstan State Statistics Agency 2013). A further 18 million ha of cropland are currently abandoned in the steppe zone of Russia (Federal Governmental Statistical Service Russia 2013; Smelanskii 2012). In Kazakhstan (but less so in Russia) livestock numbers increased significantly since 2000, but the animals are now mostly concentrated within 10 km of human settlements due to a lack of transport facilities and watering infrastructure. This leads to a very imbalanced grazing pressure with local overgrazing around villages and absence of grazing over vast grassland expanses (Kamp et al. 2011; Robinson et al. 2003).

While a number of recent studies have shed light on the impact of post-Soviet abandonment on soil organic carbon sequestration (Kurganova et al. 2014), the implications of these socio-economic changes for biodiversity and restoration are still poorly understood (Kamp 2014).

Agricultural abandonment provides unique opportunities for restoring native steppe grassland systems and their biodiversity (Gerla et al. 2012). While there is evidence that populations of some bird species have recovered on abandoned land (Herzon et al. 2014; Kamp et al. 2011, 2012), hardly any information is available whether restoration of native steppe grassland vegetation in Kazakhstan and Russia is possible by spontaneous succession. Given the large-scale and almost complete destruction of the native steppe grassland vegetation by arable cultivation, seed and dispersal limitation as well as changes in site conditions as a legacy of past land-use must be considered as major obstacles for the restoration of the original species composition and vegetation structure. Another severe change in environmental conditions arises from the dramatic decline of livestock and wild ungulates after the collapse of the Soviet Union leading to large areas without any grazing in the steppe region. Research from the north American prairies has shown that grazing and fire are the major determinants of plant community composition and structure in temperate grasslands (Bond and Keeley 2005; Collins and Smith 2006; Knapp et al. 1999). Species-richness and diversity usually peak in areas with a balanced interplay between fire and grazing. Recently burned areas are preferentially grazed by large herbivores (Fuhlendorf and Engle 2004). The complete absence of grazing leads to an accumulation of thick plant litter layers facilitating higher fire recurrence rates and higher fire temperatures (Collins and Calabrese 2012; Fuhlendorf et al. 2009), which in turn decreases floristic diversity (e.g. Ruprecht et al. 2010). An increasing fire recurrence rate due to litter accumulation that resulted from declining livestock numbers has been demonstrated for the steppes of Kalmykia in southern Russia (Dubinin et al. 2011). Efficient long-distance seed dispersal and the creation of suitable microsites for germination are also negatively affected when grazer numbers decline (Bakker and Olff 2003). Abiotic (altered soil conditions) and biotic constraints (depleted seed banks, dispersal limitation, absence of grazers) in spontaneous succession can lead to impoverished or novel species compositions and/or systems with altered ecosystem processes (Cramer et al. 2008; Hobbs et al. 2009; Römermann et al. 2005).

Research on temperate steppe grassland restoration on abandoned cropland is sparse in western Eurasia (Dengler et al. 2014) and biased towards the North American prairies (Fuhlendorf et al. 2009; Gerla et al. 2012). This applies especially to the importance of dispersal limitation and the interplay of grazing and fire on vegetation development that has hardly been studied within the western Eurasian steppe belt (Valkó et al. 2014). Spatial scale is another major issue that makes it difficult to transfer scientific findings, concepts and strategies from northern America to western Eurasia. In northern America, prairie restoration projects covering 9000 ha of former cropland are already considered large scale (Gerla et al. 2012) and in Western and Central Europe they are usually much smaller (Török et al. 2011). These projects are tiny spots compared to the 25 million ha of abandoned cropland within the steppe zone of Kazakhstan and Russia that are currently self-restoring via spontaneous succession. Typical active restoration measures often applied in prairie and other dry grassland restoration in western countries imply the sowing of native target plant species to overcome seed and dispersal limitation (Martin and Wilsey 2012; Török et al. 2010, 2011) as well as prescribed burning and grazing schemes to mimic natural disturbance regimes (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009). Such measures are probably not feasible under the given spatial dimensions and the socio-economic marginal conditions of steppe grassland restoration in countries of the former USSR. Thus, it appears to be even more important to obtain more detailed information about the results and potential constraints of this currently by far largest 'restoration project' in a natural habitat on earth that is so far completely based on spontaneous succession.

We compared vegetation composition and abiotic site conditions on former cereal fields on the Kazakh steppe that were abandoned between 1991 and 1995 to those on near-natural steppe sites that had never been ploughed. We aimed to assess: (i) how vegetation on abandoned arable fields differs from near-natural steppe grassland vegetation after 15–20 years of abandonment, (ii) which environmental factors influence the establishment of steppe vegetation on abandoned cropland and (iii) how grazing influences the establishment of steppe vegetation on abandoned cropland.

Materials and methods

Study region

Fieldwork was conducted in Kazakhstan's Akmola province, around the village Korgalzhyn (50°35′N; 70°00′E), in a region characterised by flat short-grass steppe, used and abandoned arable fields and numerous shallow saline and freshwater lakes (Kamp et al. 2011). The climate is strongly continental. The average annual temperature is 2.8 °C, but in the hot summers, temperatures can exceed 40 °C, whereas the cold and dry winters reach temperatures of −50 °C. With an average annual precipitation total of 267 mm (Korgalzhyn weather station, means 1970–2010, Kamp et al. 2011), the study region is situated just north of the southern border of rain-fed agriculture (250 mm precipitation isoline). Arable agriculture is dominated by rain-fed cereal farming, with ca. 95 % of the arable area sown with spring wheat. Precipitation varies strongly between years and droughts occur periodically. Due to the low level (on average 5dt/ha) and uncertainty of yields as well as financial and application problems the use of mineral fertilizer and pesticides is rare. Dominating soils in the area are light and medium Kastanozems (chestnut soils) of variable carbonate content, often mixedwith solonetz and solonchaks soils in depressions. The steppe vegetation is characterised by fescue-feather grass steppe with the grasses *Festuca valesiaca, Stipa lessingiana* and *S. capillata* as well as several wormwood species (*Artemisia* spp.). Parts of the region are grazed with low to moderate livestock densities, but hardly any wild ungulates were present with the exception of few (<50) Saiga antelopes *Saiga tatarica*.

The vegetation of abandoned cereal fields and near-natural steppe was studied on two former state farms (Sovkhoz) that differed in recent management history but also soil characteristics: The former state farm "Druzhba" (ca. 91,000 ha) to the north around the village Korgalzhyn comprised near-natural steppe (31 %) and abandoned cereal fields (22 %) on calcium carbonate-poor, sandy-loamy substrate. Steppe remnants are irregularly dispersed mostly in pockets and transitions between abandoned fields (usually 2 × 2 km) and areas unsuitable for cropping (e.g. on steeper slopes or in saline depressions). The area was grazed in a community herding scheme (cattle, horses and sheep/goats) and partly free ranging herds of horses. Strongly overgrazed areas around village were excluded from sampling. Until the late 1990s there was a tremendous decline of livestock. Since then numbers have recovered, specifically the number of horses, which are particularly relevant for our study, almost doubled between 1999 and 2010 (Kamp et al. 2011, 2012).

A second southern study area, ca. 50 km to the south-east of Korgalzhyn comprised the eastern part of the former state farm 'Kurgaldzhinskii' (ca. 65,000 ha), made up by 36 % of near-natural steppe and 27 % of abandoned arable fields. Soils in this area were characterised by a heavier texture, with higher calcium carbonate content in the topsoil and a higher degree of salinity in deeper soil layers compared to the first study area. In this area a relatively compact block of abandoned fields (ca. 30 × 10 km) was chosen for vegetation sampling, which was surrounded near-natural steppe. Grazing ceased shortly after the collapse of the Soviet Union in 1991 and the following human depopulation, and the area is since then only occasionally visited by herds of semi-wild horses.

To analyse the impact of grazing by free roaming livestock under real world conditions at landscape scale it was indispensable to spatially split grazing treatments. As in other grazing experiments realism and the long-term nature of treatments make this the only reasonable and feasible design to assess the effects of grazing and associated processes such as fire at this spatial scale (Collins and Calabrese 2012). Abiotic site conditions were studied at plot level to analyse and account for potentially confounding effects.

Vegetation sampling

Between 21 May and 25 June 2011, vegetation was sampled on 62 plots in near-natural (i.e. never ploughed) steppe and 89 plots in abandoned cereal fields. 75 plots (30 on steppe, 45 on abandoned fields) were selected in the northern study area and 76 plots (32 on steppe, 44 on abandoned fields) in the southern one. We restricted our study to fields that were abandoned between 1991 and 1995 and were not ploughed since. As complete random sampling was not feasible for logistical reasons, we set up an approximately regular sampling design: driving along dust tracks, we stopped every 500 m and selected a sampling plot in an orthogonal distance of 100 m to the track. For 43 sampling locations (25 in the north, 18 in the south), abandoned plots were paired with near-natural steppe plots (along tracks that had abandoned fields on one site and near-natural steppe on the other), the remaining plots were selected keeping the same distances as given above in larger steppe remnants and areas of contiguous abandoned fields. Steppe sites that showed signs of salinization (indicated by polygonal desiccation cracks, salt crusts and plant species composition) were excluded as these are unsuitable for arable use.

At each sampling plot we recorded abundance for all vascular plant species following the extended Braun-Blanquet cover-abundance scale (Dierschke 1994) in a quadrat of 10 × 10 m. Taxonomy follows The Plant List (2013), species were classified e.g. as steppe specialists (later on called steppe species), ruderal weeds etc. (Table S1) following Karamysheva and Rachkovskaya (1973). As dung has been shown to be a good correlate of grazing intensity (Laing et al. 2003), dung piles of cattle, horses and sheep were counted along a strip transect of 100 m length and 2 m width and later pooled, centred on each vegetation quadrat. The topsoil was sampled with five cores (N-min corer of 3 cm in diameter) to a depth of 10 cm. To estimate productivity, chemical characteristics and the nutritional value of the vegetation, green aboveground biomass was harvested on five 0.25 m^2 quadrats. Litter and dead plant material were sorted out. Biomass and soil samples were collected at all four edges of the 10 × 10 m sample plot and in the centre of each plot, and pooled afterwards.

Sample processing and laboratory analyses

Soil samples were air-dried and then sieved to 2 mm. Soil pH-values were measured in a 1:2.5 soil-calcium chloride solution using a glass electrode pH meter. Electrical conductivity (EC) was measured in a 1:10 soil/distilled water solution. $CaCO_3$ content was measured using the gas volumetric Scheibler method and used as a correlate of inorganic carbon content in analysis. Carbon (C) and nitrogen (N) content of the soils samples was determined using a EuroEA CHNS-O elemental analyzer (HEKAtech GmbH Analysentechnik, Wegberg, Germany).

Total carbon minus the $CaCO_3$-carbon gives the organic carbon in the soil. This was used to calculate the content of organic matter in the soil samples and the C/N-ratio. To determine plant-available phosphorus (P) and potassium (K) soil samples were extracted with calcium-acetate-lactate (CAL) (Hoffmann 1991) and measured photometrically.

Plant biomass samples were air-dried at 60 °C for 48 h and weighed afterwards. They were then chaffed and ground to pass a 0.5 mm sieve and air-dried again at 60 °C for 12 h. Using a near-infrared reflectance spectrometer (Spectra Star 2400, Unity Scientific, Columbia, MD, USA), the samples were then analysed for calcium (Ca), carbon, magnesium (Mg), nitrogen, phosphorus (P) and potassium (K) contents as well as neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL). The latter are indicators of the nutritional value of grassland biomass. In 1 nm intervals, the samples were scanned over a range of wavelengths from 1250 to 2350 nm and established and well-tested calibration models for a wide range of temperate grassland biomass (Kleinebecker et al. 2012) were used.

Data analysis

We tested for differences in the means of the characteristics of grazed and ungrazed abandoned fields and near-natural steppe using one-way ANOVAs where the data were normally distributed, and non-parametrical Kruskal–Wallis tests where they were not. If significant, post hoc tests were used to assess differences in group means. An Indicator Species Analysis (Dufrêne and Legendre 1997) was performed in PC-ORD 5.0, which takes account of relative frequencies and abundances of each species in each sample-type. The indicator value of a species is evaluated for a group of samples by the multiplication of its relative abundance within a particular group over all groups and its relative frequency within the particular group, both expressed as percentages. Significant differences between the indicator value of a species within a particular group and the expected average mean over all groups are tested by Monte Carlo statistics with a large number (1000) of random runs (McCune and Mefford 1999).

Relationships between the plant community composition and environmental parameters were visualised using a Principal Component Analysis (PCA) for vegetation structure and life form composition and a Detrended Correspondence Aanlysis (DCA) for species composition and environmental parameters. Log-transformed and standardised (z-transformation) environmental data were used as an overlay. In order to isolate the effect of grazing on species composition on abandoned fields and to account for confounding soil effects we performed a decomposition of variance by running a series of partial CCAs as proposed by ter Braak and Šmilauer (2012, p. 279ff). In all multivariate analyses, species cover values were square-root transformed.

To compare the impact of potential drivers of re-colonisation of abandoned fields by steppe species, we modelled species richness and cover of steppe species as a function of three variables that were proposed earlier to have an influence on species composition on abandoned arable fields in the Kazakh steppe and other dry grassland ecosystems: Soil $CaCO_3$ content and electric conductivity (Marinych et al. 2002) and grazing intensity (Gibson et al. 1987). As these three factors were confounded within both the ungrazed southern and the grazed northern study plots, we restricted the analysis to the plots of the northern study site. We fitted negative binomial (as the data were overdispersed) Generalized Linear Models (GLMs) to the count and cover data using library MASS in R 3.0.1. Models were compared using AIC_C and ranked according to their Akaike-weights (Burnham and Anderson 2002).

Results

Our analyses revealed a significantly higher calcium carbonate content in the soils of the southern study area, which was also reflected by higher electric conductivity and pH-value in the soil solution (Table 1). Other soil properties such as total organic carbon, total nitrogen, C/N-ratio and plant available potassium were not significantly different between the northern and the southern study area. Plant available phosphorus content was significantly higher in the southern area. Across both study areas, the only soil variable that showed constant differences between near-natural steppe grassland and ex-arable land was organic carbon content, which was ca. 25 % lower in abandoned fields (Table 1). For total N such differences were only found in the north where abandoned fields exhibited less N, but slightly raised levels of plant-available P compared to near-natural steppe. Our assumptions of moderate grazing levels in the northern study area and a nearly complete absence of grazing in the southern area were clearly confirmed by the dung pile counts (Table 1). More than 80 % of the dungs piles were of horse origin.

Near-natural steppe grassland in the north and the south showed great similarity in terms of vegetation structure and functional group composition (Table 2; Fig. 1). However, there were also some obvious differences in floristic composition (Fig. 2). Several species avoiding alkaline conditions such as *Stipa zalesskii, Eremogone longifolia, Valeriana tuberosa* and *Galium verum* as well as species with a preference for more sandy substrates such as *Artemisia marschalliana* and *Gypsophila paniculata* (Karamysheva and Rachkovskaya 1973) were exclusively or in higher abundances found in the north, whereas species tolerating more alkaline conditions such as *Serratula kirghisorum, Tanacetum achillefolium, Palimbia salsa* and *Ferula caspica* occurred more frequently and in higher abundances in the south (Table 3), reflecting the higher soil pH and electric conductivity in

Table 1 Means and standard errors of soil and site parameters in near-natural steppes and on abandoned arable fields of both study areas

	Near-natural steppe		Abandoned fields	
	North-grazed 30	South-ungrazed 32	North-grazed 45	South-ungrazed 44
Soil properties				
EC (µS/cm)	57.6 ± 6.3^{b}	105.3 ± 2.2^{a}	35.4 ± 2.7^{c}	152.7 ± 40.4^{a}
pH-value	6.3 ± 0.1^{b}	7.5 ± 0.0^{a}	6.4 ± 0.1^{b}	7.5 ± 0.0^{a}
$CaCO_3$ (%)	1.2 ± 0.5^{b}	7.8 ± 0.8^{a}	0.1 ± 0.0^{b}	9.7 ± 0.6^{a}
C (%)				
Total	1.8 ± 0.1^{b}	2.6 ± 0.2^{a}	1.3 ± 0.1^{c}	2.5 ± 0.1^{a}
Inorganic	0.1 ± 0.1^{b}	0.9 ± 0.1^{a}	0.0 ± 0.0^{b}	1.2 ± 0.1^{a}
Organic	1.7 ± 0.1^{a}	1.7 ± 0.2^{a}	1.3 ± 0.1^{b}	1.3 ± 0.1^{ab}
OM (%)	2.9 ± 0.2^{a}	2.9 ± 0.3^{a}	2.2 ± 0.3^{b}	2.3 ± 0.2^{ab}
N (%)	0.2 ± 0.0^{a}	0.2 ± 0.0^{a}	0.1 ± 0.0^{b}	0.2 ± 0.0^{a}
C/N-ratio	10.5 ± 0.3^{a}	8.4 ± 0.7^{ab}	10.3 ± 0.5^{ab}	8.1 ± 0.5^{b}
P-CAL (mg/100 g)	0.9 ± 0.1^{c}	2.4 ± 0.3^{a}	1.2 ± 0.1^{b}	2.4 ± 0.3^{a}
K-CAL (mg/100 g)	24.3 ± 2.1^{a}	20.4 ± 2.1^{a}	22.4 ± 1.0^{a}	24.9 ± 1.9^{a}
Dung piles/200 m^2	17.4 ± 2.0^{a}	0.5 ± 0.2^{b}	17.0 ± 1.5^{a}	0.0 ± 0.0^{b}

Subscript letters indicate significant differences ($p < 0.05$) after non-parametric Dunn's Method

Table 2 Means and standard errors of vegetation and biomass-related parameters

	Near-natural steppe		Abandoned fields	
	North-grazed 30	South-ungrazed 32	North-grazed 45	South-ungrazed 44
Species richness				
Total	24.1 ± 1.0^{a}	18.8 ± 0.7^{b}	22.8 ± 0.8^{ab}	11.6 ± 0.7^{c}
True steppe species	20.5 ± 0.8^{a}	17.7 ± 0.7^{a}	11.4 ± 0.5^{b}	5.0 ± 0.3^{c}
Ruderal weeds	2.9 ± 0.4^{c}	0.9 ± 0.2^{c}	10.5 ± 0.6^{a}	6.6 ± 0.6^{b}
Indifferent species	0.6 ± 0.1^{ab}	0.2 ± 0.1^{bc}	0.8 ± 0.2^{a}	0.1 ± 0.0^{c}
Annuals	2.2 ± 0.3^{b}	0.6 ± 0.2^{c}	4.6 ± 0.5^{a}	4.4 ± 0.4^{a}
Legumes	1.4 ± 0.2^{a}	0.6 ± 0.2^{b}	2.2 ± 0.2^{a}	0.2 ± 0.1^{b}
Dwarf shrubs	3.7 ± 0.2^{ab}	3.2 ± 0.2^{b}	4.1 ± 0.1^{a}	1.0 ± 0.2^{c}
Grasses (perennial)	4.5 ± 0.3^{a}	4.1 ± 0.2^{a}	3.8 ± 0.2^{a}	2.4 ± 0.1^{b}
Herbs (perennial)	12.4 ± 0.7^{a}	10.3 ± 0.6^{ab}	8.0 ± 0.4^{b}	3.5 ± 0.4^{c}
Diversity estimators				
Shannon	2.4 ± 0.0^{a}	2.1 ± 0.1^{b}	2.3 ± 0.1^{ab}	1.2 ± 0.1^{c}
Evenness	0.8 ± 0.0^{a}	0.7 ± 0.0^{a}	0.7 ± 0.0^{a}	0.5 ± 0.0^{b}
Vegetation cover (%)				
Total	48.0 ± 2.1^{ab}	42.2 ± 1.7^{b}	48.2 ± 1.1^{ab}	53.6 ± 2.1^{a}
True steppe species	94.2 ± 1.1^{a}	96.7 ± 1.1^{a}	62.0 ± 3.0^{c}	82.0 ± 3.1^{b}
Ruderal weeds	4.5 ± 0.9^{c}	3.2 ± 1.0^{c}	36.3 ± 2.9^{a}	18.0 ± 3.1^{b}
Indifferent species	1.3 ± 0.4^{ab}	0.2 ± 0.1^{bc}	1.7 ± 0.5^{a}	0.0 ± 0.0^{c}
Annuals	2.1 ± 0.4^{b}	0.9 ± 0.4^{b}	9.4 ± 1.4^{a}	13.5 ± 2.5^{a}
Legumes	$2.1 \pm \pm 0.4^{b}$	0.7 ± 0.2^{c}	6.3 ± 0.9^{a}	0.3 ± 0.1^{c}
Dwarf shrubs	14.4 ± 1.7^{b}	16.7 ± 1.7^{b}	35.1 ± 2.6^{a}	3.3 ± 1.0^{c}
Grasses (perennial)	45.8 ± 1.8^{bc}	48.6 ± 2.1^{b}	32.5 ± 2.7^{c}	77.1 ± 3.3^{a}
Herbs (perennial)	35.5 ± 2.0^{a}	33.1 ± 2.1^{a}	16.7 ± 1.6^{b}	5.8 ± 0.9^{c}
Cover of bare ground (%)	27.8 ± 2.9^{c}	41.3 ± 1.9^{a}	38.2 ± 1.8^{ab}	29.9 ± 2.4^{bc}
Vegetation height (cm)				
Average	19.3 ± 0.8^{a}	21.3 ± 0.8^{a}	18.3 ± 1.2^{a}	20.2 ± 0.5^{a}
Maximum	19.3 ± 0.8^{b}	22.2 ± 1.1^{b}	37.6 ± 1.8^{a}	23.2 ± 1.4^{b}
Yield (g/m^2)	61.6 ± 5.1^{ab}	49.7 ± 3.1^{b}	61.2 ± 2.4^{a}	59.7 ± 4.2^{ab}
Biomass contents (%)				
NDF	49.3 ± 1.6^{BC}	51.5 ± 1.5^{B}	44.1 ± 1.2^{C}	55.8 ± 1.0^{A}
ADF	32.0 ± 0.5^{a}	32.2 ± 0.6^{a}	31.1 ± 0.3^{a}	32.6 ± 0.4^{a}
ADL	7.2 ± 0.2^{a}	6.9 ± 0.2^{a}	7.8 ± 0.2^{a}	5.6 ± 0.1^{b}
C	49.5 ± 0.2^{a}	49.4 ± 0.2^{a}	48.7 ± 0.1^{b}	49.4 ± 0.2^{a}
Ca	1.3 ± 0.1^{AB}	1.1 ± 0.1^{B}	1.4 ± 0.1^{A}	0.8 ± 0.1^{C}
K	0.9 ± 0.1^{B}	1.1 ± 0.1^{AB}	1.2 ± 0.1^{AB}	1.4 ± 0.1^{A}
Mg	0.2 ± 0.0^{ab}	0.2 ± 0.0^{bc}	0.2 ± 0.0^{a}	0.1 ± 0.0^{c}
N	2.4 ± 0.1^{ab}	2.4 ± 0.1^{ab}	2.3 ± 0.0^{b}	2.6 ± 0.1^{a}
P	0.2 ± 0.0^{B}	0.2 ± 0.0^{B}	0.2 ± 0.0^{B}	0.2 ± 0.0^{A}

Subscript letters indicate significant differences ($p < 0.05$). Capitalised letters indicate post hoc-testing with Tukey-tests, lower case letters using non-parametric Dunn's Method

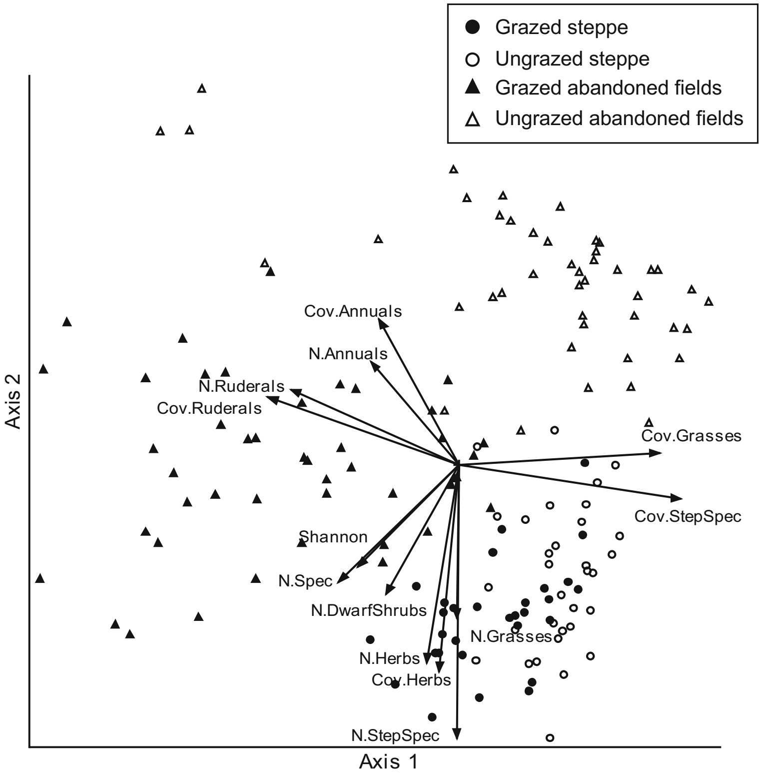

Fig. 1 PCA ordination diagram displaying structural and compositional differences in life forms of near-natural steppe and abandoned arable fields in the northern (grazed) and southern (ungrazed) study area

this area (Fig. 2). Unlike near-natural steppe grassland, abandoned arable fields showed profound differences in vegetation structure and composition between the two study areas (Table 2; Fig. 1). In the north, abandoned fields were dominated by dwarf shrubs of the genus *Artemisia* and ruderal weeds. Contrarily, in the south few perennial grasses such as *Stipa lessingiana* and *Leymus ramosus* dominated (Fig. S1; Table 3), whereas ruderals were less abundant and dwarf shrub cover was insignificant (Tables 2, 3; Fig. 1). Legumes and other perennial herbs reached a lower cover compared to the northern study area. Besides, several species of wormwood such as *A. austriaca* and *A. nitrosa*, grazing-resistant legumes such as *Astragalus testiculatus* and *A. macropus* and short grasses such as *Festuca valesiaca* and *Koeleria macrantha* reached high frequency and cover on the abandoned fields of the northern study area (Table 3) whereas they were almost completely absent in the southern area. Tall grasses preferentially selected by grazing livestock such as *Stipa lessingiana* were comparatively infrequently recorded and occurred only in low cover in the north (Table 3). Total plant species richness in abandoned fields was twice lower in the south compared to the north, where similar levels like in near-natural steppe grasslands were achieved (Table 2). While aboveground productivity did not differ significantly between abandoned fields in the south and the north, differences in life form composition were clearly reflected in biomass quality properties such as NDF, ADL, Ca, Mg, N and P

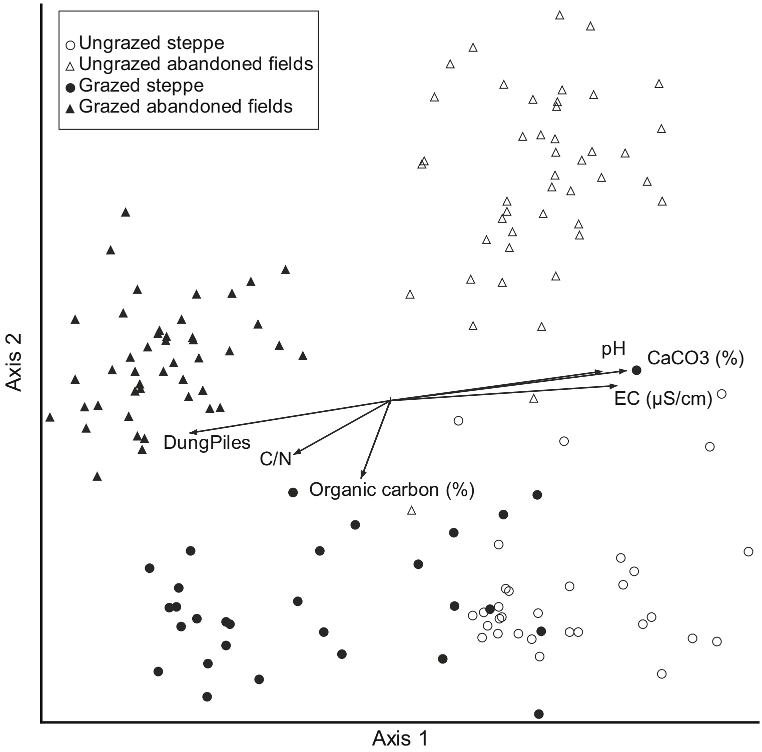

Fig. 2 DCA ordination diagram displaying differences in species composition and correlation with environmental variables of near-natural steppe and abandoned arable fields in the northern (grazed) and southern (ungrazed) study area

(Table 2). The values of these parameters were significantly higher in the ungrazed abandoned fields in the south than in the grazed area in the north.

In a constrained ordination, $CaCO_3$ content and pH value were identified by forward selection as the most important explanatory soil variables. Together with the density of dung piles they explained 21.18 % of the total variation in the species data of abandoned fields in both test areas. Dung piles alone explained 12.2 % whereas $CaCO_3$ content and pH together accounted for 19.32 % the of species variation, indicating a high proportion of shared variance (10.34 %) between the soil factors and dung pile density. However, even after accounting for $CaCO_3$ content and soil pH in partial CCA, dung pile density as a proxy of grazing intensity was still highly significant and accounted for 2.3 % of the remaining species variance.

After 15–20 years of spontaneous succession, abandoned arable fields still differed significantly from near-natural steppe, in terms of structure, functional characteristics and floristic composition (Table 2; Figs. 1, 2). Many typical steppe plant species have so far not colonized the former arable fields. This was particularly true for the ungrazed plots: While the number of steppe species at grazed abandoned fields already comprised 56 % of corresponding near-natural steppe sites, this figure was only 28 % for the ungrazed and grass-dominated abandoned fields in the south (Table 2). This pattern became also visible in a greater proximity of northern samples from steppe and abandoned fields in ordination

Table 3 Indicator species analysis for near-natural steppes and abandoned arable fields of both study areas

Sample-type	IV	*p*	Near-natural steppe		Abandoned fields	
n			North-grazed 30	South-ungrazed 32	North-grazed 45	South-ungrazed 44
Galatella villosa	**73.5**	***	*83/72*	22/7	56/20	5/1
Ferula tatarica	**69.4**	***	*73/83*	22/15	4/2	–
Tulipa patens	**58.0**	***	*70/58*	56/30	2/1	20/11
Stipa zalesskii	53.2	***	*53/99*	–	2/1	–
Eremogone longifolia	42.8	***	*43/97*	–	2/3	–
Valeriana tuberosa	42.4	***	*43/94*	3/4	2/3	–
Stipa capillata	36.3	**	*53/42*	16/17	33/23	27/19
Scorzonera austriaca	31.1	**	*43/44*	34/29	4/3	18/24
Verbascum phoeniceum	30.4	***	*33/78*	3/6	4/16	–
Carex stenophylla	29.3	***	*30/94*	–	2/6	–
Ephedra distachya	26.7	***	*27/100*	–	–	–
Poa bulbosa	26.7	***	27/100	–	–	–
Allium flavescens	24.0	**	*30/54*	19/32	9/13	–
Sisymbrium polymorphum	22.7	***	*27/62*	16/29	2/4	2/4
Bassia prostrata	**82.6**	***	33/25	*94/47*	13/5	7/3
Galatella tatarica	**77.1**	***	50/22	*97/55*	51/12	32/10
Serratula kirghisorum	**76.5**	***	27/22	*84/73*	–	16/5
Tanacetum achilleifolium	**72.1**	***	37/18	*81/70*	16/7	9/4
Palimbia salsa	**68.3**	***	30/36	*78/64*	–	–
Eremogone procera	53.4	***	23/29	*59/70*	–	2/2
Ferula caspica	52.6	***	33/32	*59/67*	–	2/2
Psathyrostachys juncea	50.5	***	10/15	*53/83*	–	2/2
Serratula dissecta	49.1	***	3/4	*50/94*	–	2/2
Artemisia semiarida	42.0	***	3/7	*44/88*	–	5/5
Iris scariosa	32.8	***	3/11	*38/69*	–	11/19
Artemisia pauciflora	26.6	***	7/15	*28/82*	–	2/3
Phlomis tuberosa	**67.7**	***	*73/54*	*63/46*	–	–
Jurinea multiflora	**56.5**	***	*60/48*	*53/52*	–	–
Pedicularis physocalyx	30.6	***	*33/56*	*28/44*	–	–
Artemisia marschalliana	**93.2**	***	27/8	–	*96/92*	–
Convolvolus arvensis	**86.9**	***	3/1	–	*98/76*	36/22
Gypsophila paniculata	**79.0**	***	57/31	–	*89/69*	–
Astragalus testiculatus	**74.0**	***	30/18	19/8	*82/73*	2/1
Koeleria macrantha	**69.1**	***	50/21	47/20	*84/57*	5/1
Achillea nobilis	**64.5**	***	3/2	3/4	*71/79*	16/15
Artemisia dracunculus	**62.6**	***	20/19	–	*67/81*	–
Agropyron cristatum	**58.7**	***	27/11	63/28	*76/52*	20/8
Artemisia nitrosa	**56.0**	***	43/18	34/20	*78/46*	45/16
Silene wolgensis	52.7	***	10/12	–	*56/85*	2/3
Alyssum turkestanicum	52.0	***	43/23	6/3	*67/55*	27/18

Table 3 continued

Sample-type	IV	*p*	Near-natural steppe		Abandoned fields	
n			North-grazed 30	South-ungrazed 32	North-grazed 45	South-ungrazed 44
Chenopodium album	39.2	***	20/21	–	*42/79*	–
Nonea pulla	31.1	***	–	–	*31/100*	–
Medicago falcata	28.7	***	7/17	3/5	*31/77*	–
Poa versicolor	20.5	***	7/17	3/5	*22/77*	–
Onosma tinctoria	20.0	***	–	–	*20/100*	–
Atriplex aucheri	48.1	***	–	–	16/17	*52/83*
Lappula patula	44.7	***	–	3/2	20/27	*52/71*
Lappula consanguinea	36.6	***	7/8	3/2	33/34	*48/71*
Salsola tamariscina	28.2	***	3/3	6/10	13/14	*32/73*
Brassica elongata subsp. integrifolia	26.7	***	3/6	3/5	13/23	*32/66*
Bassia sedifolia	**58.6**	***	23/8	3/2	*62/46*	*68/44*
Taraxacum officinalis agg.	37.2	***	10/8	–	*44/41*	*36/51*
Lactuca tatarica	30.3	***	–	–	*36/52*	*25/48*
Descurainia sophia	23.8	*	*23/19*	6/8	*29/33*	*34/40*
Festuca valesiaca	**83.0**	***	*87/42*	41/10	*93/48*	2/0
Artemisia austriaca	**71.7**	***	*93/29*	72/18	*96/44*	36/8
Astragalus macropus	**60.5**	***	*67/37*	22/12	*73/47*	9/4
Erysimum leucanthemum	48.0	***	*47/39*	13/10	*58/50*	2/2
Galium verum	47.9	***	*60/56*	6/5	*44/38*	2/1
Potentilla humifusa	36.1	***	*47/44*	13/12	*36/45*	–
Stipa lessingiana	**73.1**	***	43/18	*91/39*	38/7	*98/37*
Leymus ramosus	**67.6**	***	47/13	*78/22*	18/4	*80/61*

For each species the percentage frequency and percentage of total abundance within the corresponding type is given. The first column (IV) shows the maximum indicator value (in italics) over all types for the framed section. Indicator values in the second column refer to the framed column sections. Species with non-significant or low indicator value (IV $\leq$ 20) are not shown. Species with high indicator values (IV $\geq$ 55) are given in bold

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

space (Fig. 2). On the contrary, total cover of typical steppe species was significantly higher in the ungrazed southern study area, but was made up by solely two dominant grass species, *Stipa lessingiana* and *Leymus ramosus* (Tables 2, 3).

There were big differences in establishment success between individual steppe target species (Table 3). While some taxa such as *Festuca valesiaca, Koeleria macrantha, Astragalus testiculatus, Galatella tatarica, G. villosa, Stipa lessingiana* and *S. capillata* were particularly successful colonizers, others were never, e.g. *Phlomis tuberosa, Jurinea multiflora, Pedicularis physocalyx, Palimbia salsa*, or only in single occasions found in abandoned arable fields, e.g. *Eremogone procera, Ferula caspica, Serratula dissecta.*

Model selection results suggested that grazing intensity had a stronger influence on species richness and cover of steppe species in abandoned fields of the northern area than Calcium carbonate content and electric conductivity (Table 4), although model fit was poor and there was large variation in the data (Fig. 3). In the full model, site (i.e. near-natural

Table 4 Competing negative binomial GLMs explaining variation in species richness of steppe plant species across plots of the northern study area (grazed, lower salinity and carbonate content, ranked by AIC_C)

Model	Intercept	Dung	$CaCO_3$	EC	Site	AIC_C	ΔAIC_C	w_i
Species richness of steppe plants								
1	2.894	0.007159			+	400.2	0.000	0.362
2	2.931	0.00613	−0.017		+	401.4	1.200	0.198
3	2.873	0.00749		0.00028	+	402.5	2.240	0.118
4	2.828	0.007294	−0.031	0.00172	+	402.5	2.320	0.114
5	3.051		−0.0268		+	403.0	2.790	0.090
6	3.022				+	403.9	3.630	0.059
7	3.021		−0.0327	0.00064	+	405.1	4.890	0.031
8	3.074			−0.0009	+	405.4	5.160	0.027
Cover of steppe plants								
1	4.432	0.006643			+	664.8	0.000	0.322
2	4.398	0.007498	0.0158		+	666.2	1.410	0.159
3	4.526	0.006178	0.0341	−0.0022	+	666.5	1.740	0.135
4	4.482	0.005954		−0.0007	+	666.8	2.020	0.117
5	4.545				+	667.3	2.530	0.091
6	4.637			−0.0016	+	667.8	2.970	0.073
7	4.684		0.0323	−0.0031	+	667.8	3.010	0.072
8	4.54		0.004		+	669.5	4.700	0.031

Dung—dung abundance along a 100 m-strip transect, $CaCO_3$—soil Calcium carbonate content, EC—electrical conductivity. ‘Site’ was entered in all models as a two-level fixed factor (abandoned field vs. near-natural steppe)

AIC_C Akaike information criterion corrected for small sample size, ΔAIC_C AIC_C difference to the best model, w_i Akaike weight

steppe vs. abandoned field) was a highly significant predictor of both species richness (parameter estimate −0.579329 ± 0.065SE, $p < 0.001$ for abandoned) and cover (parameter estimate −0.435205 ± 0.064847SE, $p < 0.001$), suggesting again large differences between near-natural steppe and abandoned field plots of the northern study area (Fig. 3).

Discussion

The results of our study suggest that abandoned arable fields in central Kazakhstan are developing back into steppe 15–20 years after abandonment by spontaneous succession, which was already expected by Dieterich (2000) in the late 1990s. However, the process seems slow and steppe vegetation communities on abandoned fields are far from being similar to near-natural steppe (Figs. 1, 2; Tables 2, 3). Our results are in line with findings from dry grassland restoration projects in other regions in Europe and North-America, which reported slow and incomplete recovery of grassland vegetation on abandoned cropland even after decades (Kindscher and Tieszen 1998; Martin and Wilsey 2012; Redhead et al. 2014; Römermann et al. 2005; Ruprecht 2005; Sojneková and Chytrý 2015;

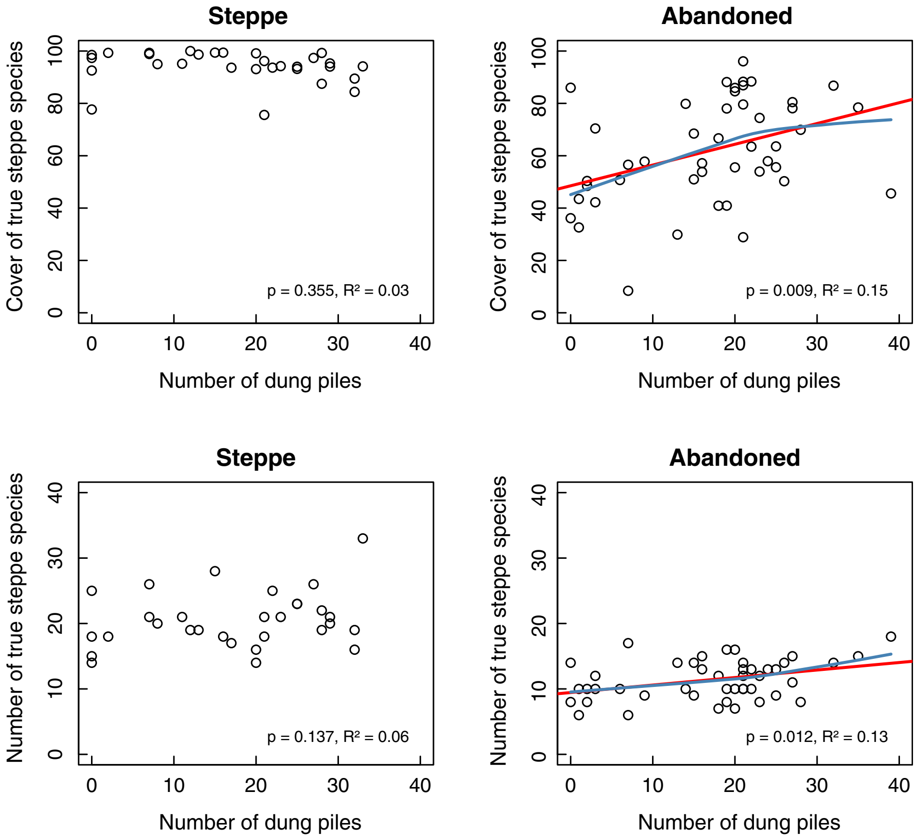

Fig. 3 Species richness and cover of steppe plants across plots of the northern study area (grazed, low salinity and carbonate content) in relation to grazing intensity as estimated by dung abundance (dung piles per 100 m strip transect). Lines are linear regressions (*red*) and Locally Weighted Scatterplot Smoothing LOWESS plots (*blue*). (Color figure online)

Veldman et al. 2015). In our study we found no indication that restoration was hampered by abiotic constraints such as soil nutrient status or salinity. There were only minor differences in soil factors between near-natural steppe and abandoned fields except for significantly lower concentrations of topsoil organic carbon in the latter due to losses in the course of arable cultivation. These values are in line with the values reported by Kurganova et al. (2014) for abandoned arable fields on Kastanozems in Russia. Similarly there were no significant differences in vegetation height and aboveground biomass yield between near-natural steppe and abandoned fields (Table 2). Thus, we can rather assume biotic constraints such as seed, dispersal and micro-site limitations, which were found as major causes of limited restoration success also in many European grassland restoration projects (Bakker and Berendse 1999; Hölzel et al. 2012).

Abandoned arable fields exhibited profound differences between the study areas in successional pathways. While grazed arable fields in the north were dominated by dwarf shrubs of the genus *Artemisia*, ruderal weeds, grazing resistant shortgrasses, abandoned arable fields in the south were dominated by two tall grass species, *Stipa lessingiana* and *Leymus ramosus* (Fig. S1), and almost devoid of dwarf shrubs (Fig. 1; Tables 2, 3). We interpret these contrasting patterns as a result of the absence of any grazing during vegetation formation in the southern test area (Fig. S2). In temperate grasslands, the complete absence of grazing leads to a dominance of tall-growing grasses and the accumulation of plant litter (Enyedi et al. 2008). Both factors can increase frequency and severity of wildfires, which in turn boost the dominance of tall grasses (Collins and Calabrese 2012). Woody dwarf shrubs suffer most under more regular and intense fires, which may lead to a strong reduction or even exclusion of this life form (Rabotnov 1995). In fact, only in the southern study area, we found large tracts of freshly burnt grasslands on abandoned fields sometimes comprising several hundred hectares (Fig. S3). The contrasting vegetation patterns we found in this study are consistent with many fire-grazing studies in North-American Prairies (Burns et al. 2009; Collins 1992; Knapp et al. 1999). Similarly the sensitivity of *Stipa* towards grazing and its facilitation by regular fire is well established in the Russian literature (Rabotnov 1995). Vice versa, dwarf shrubs of the genus *Artemisia*, which are the main antagonists of grasses at the dry edge of the steppe gradient, are well known of being favoured by high grazing pressure but sensitive towards fire in a matrix of grasses (Walter and Breckle 1994). One may argue that the observed successional differences between abandoned fields in the north and the south are due to certain differences in soil chemical conditions between both areas.

Even after accounting for soil variables such as pH and $CaCO_3$ content in partial constrained ordination, we still found a significant effect of grazing on the floristic composition of abandoned arable fields. Our results are indicating that the mentioned soil parameters had a significant effect on species composition but they cannot explain the strongly divergent dominance structures between grazed and ungrazed abandoned fields. In case of raised alkalinity, one would expect a higher proportion of dwarf shrubs (*Artemisia*) and annuals such as *Alyssum turkestanum* and *Poa bulbosa*, which are the dominant lifeforms in semi desert environments with salty soils (Karamysheva and Rachkovskaya 1973, Golub 1994; Walter and Breckle 1994). Contrary, *Artemisia* and typical desert annuals played a minor role in the southern abandoned fields (Table 2). In fact they were much more abundant on non-alkaline but grazed plots most obvious due to their grazing resistance and the absence of fire (*Artemisia*) and the more open vegetation structure without litter accumulation (Annuals). The lack of grazing impact was less visible in near-natural steppe vegetation in the south compared to abandoned arable fields. In fact these steppe grasslands experienced grazing from their formation until the early 1990s when grazing ceased, whereas the grasslands on abandoned fields in the south never faced grazing during their successional development.

The dominance of tall grasses and the lack of woody dwarf shrubs in the ungrazed southern area is also reflected by slightly higher values of biomass quality parameters such as higher NDL, N and P and lower ADL and Ca contents (Table 2). In early summer, these currently ungrazed areas could provide fodder of similar or even better nutritional value than those currently grazed.

As demonstrated by many experiments, preferably from the American Prairies, the exclusion of grazing increases fire frequency through litter accumulation leading to the dominance of tall grasses, structural simplification, reinforced fire selection and a decline in species-richness (Collins and Smith 2006; Enyedi et al. 2008; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006). The effects of ‘pyric herbivory’ (Fuhlendorf et al. 2009) are predominantly based on the mechanism that large herbivores preferentially feed on recently burned patches with high nutritional value while they avoid neighbouring old growth that tend to accumulate litter as a fuel source for wildfires. The interaction between free roaming grazers and fire promotes a moving patch mosaic at the landscape scale that favours biodiversity and essential ecosystem functions in grasslands.

When grazing ceases completely, one essential component of this old evolutionary disturbance pattern gets lost which might have far-reaching consequences for biodiversity and ecosystem processes.

Unlike on the North-American Prairies, the interplay of fire and grazing has hardly been studied in Eurasian temperate steppe environments. For the steppes of Kalmykia in the North-Caspian lowland in southern Russia, increasing wildfire frequency and extent of area burnt has been related to the collapse of livestock numbers after the break-up of the Soviet Union (Dubinin et al. 2011). For the same region, Hölzel et al. (2002) could confirm the transformation of mixed desert steppe grass-wormwood communities into monodominant *Stipa lessingiana* stands after the cessation of grazing. Trends in livestock numbers were very similar in Kazakhstan, and results from the steppe of Kalmykia seem largely transferrable to the Kazakh steppes. Based on evidence from the North American Prairies one can assume that the complete cessation of grazing over large steppe areas and the transition to pure fire disturbance regime may lead to a decline in floristic and structural diversity within the western Eurasian steppes (Collins and Calabrese 2012; Fuhlendorf et al. 2009). This situation appears to be even more prevalent for abandoned arable fields where species enrichment may be positively influenced by grazing impact. In fact, in our study the number of colonising steppe species was significantly lower in the ungrazed southern study area (Table 2) and even within the grazed northern study area a positive effect of dung pile density on the number of colonising steppe species could be observed (Table 4; Fig. 3).

Large herbivores can enhance colonization success by reducing light competition of dominant plants (Bakker et al. 2006; Olff and Ritchie 1998), the removal of thick litter layers (Ruprecht et al. 2010) and by the creation of patches of bare soil that may serve as regenerations sites for emerging seedlings (Bakker and Olff 2003). Diaspores of many plant species can survive intake by herbivores (Cosyns et al. 2005; Malo and Suárez 1995) or attach to fur (Fischer et al. 1996), making herbivores efficient vectors for plant migration to restoration sites. All these processes potentially promoting biodiversity in abandoned fields are not operating without grazing by free roaming large herbivores.

Conclusions

In our study we found clear indications that in the complete absence of grazing, succession on abandoned fields in Kazakhstan towards natural steppe vegetation may get locked in species-poor tall grass stands dominated by *Stipa lessingiana* and *Leymus ramosus*. Whether this is a temporary phenomenon or if this process may lead to ‘novel ecosystems’ (Hobbs et al. 2009) with permanently altered species composition is still an open issue and needs clarification by future studies focusing on the long-term effects of disrupted pyric herbivory (Fuhlendorf et al. 2009) on biodiversity and ecosystem processes in Eurasian temperate steppe grasslands. The reintroduction of moderate grazing with large herbivores is likely to accelerate steppe restoration processes on abandoned fields. Grazing might reduce fire recurring rates and help to overcome seed, dispersal and microsite limitation of steppe target species. Compared to the reintroduction of grazing, other supplementary measures widely used in grassland restoration in Northern America and Europe such as the sowing of regional seed mixtures or the spread of green hay are currently not feasible given the spatial dimensions and socio-economic marginal conditions of steppe restoration in

Kazakhstan. Quantities and qualities of fodder for domestic livestock on abandoned arable land are similar or even better than in corresponding near-natural steppe grasslands. The recovery of domestic grazer stocks is currently limited by socio-economic, financial and infrastructural constraints (Robinson and Milner-Gulland 2003), while free roaming wild ungulates such as Saiga antelopes have so far not recovered from excessive poaching since the 1990s (Kühl et al. 2009; Singh and Milner-Gulland 2011). Our results also underline the uniqueness and outstanding value of 'old growth grassland' (Veldman et al. 2015) in terms of herbaceous plant diversity and species composition that deserves highest conservation priority.

Acknowledgments We thank Timur Iskakov, Edith Koshkin, Tobias Koz, Alexandr Kuzminskii, Evgeniya Senyak, Ruslan Urazaliev, Frederike Velbert and Sergey Sklyarenko for assistance with fieldwork and logistical support. Soil samples were processed by Ulrike Berning-Mader, Madeleine Supper and Melanie Tappe. This study was supported by the Royal Society for the Protection of Birds (RSPB) and funded by the UK government's Darwin Initiative (Project Ref-No. 18004) and the Volkswagen Foundation, project BALTRAK (Project Ref-No. A112025).

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